Horizontal zonation of meiobenthic copepods in the Pauatahanui Inlet, New Zealand

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Abstract

Different horizontal distributions of meiobenthic copepods were found on three transects across a variety of substrata in Pauatahanui Inlet, New Zealand. From the limited data it appears that the presence of vegetation, tidal exposure, or water depth were not common factors governing species distribution in Pauatahanui Inlet in late winter. The zonal distribution and community structure were influenced by water depth exposure in two out of three transects. Grain size was correlated with species distribution on only one transect: *Sextonis* sp. and *Parastenhelia megarostrum* were found in fine, clean sand whereas *Halectinosoma hydrofuge* and *Brianola* sp. occurred in substrate with a higher silty/clay content.

Keywords: Pauatahanui Inlet - New Zealand - salt marsh - Copepoda - meiobenthos - horizontal zonation

Introduction

The intertidal distribution of meiobenthic harpacticoid copepods is known to fall into distinct horizontal zonation patterns (e.g. Coull *et al.* 1979, Moore 1979b, see review in Hicks & Coull 1983). Distributions may be influenced by temperature, salinity, dissolved oxygen content of the interstitial water, water depth, tidal flow, tidal exposure, desiccation, microtopography, interstitial space and grain size, bacterial flora of the sediment as food source, presence or absence of macrovegetation, and the activities of macrofauna as predators and as disturbers of the sediment (Gray1968, Harris 1972a, Mielke 1976, Bell 1979, Coull *et al.* 1979, Moore 1979b, McLachlan 1980, Hockin 1982, Hicks 1986, Coull & Feller 1988). Nevertheless, Harris (1972b) considered that meiobenthic distributions in Whitsand Bay, southwest England were relatively uniform and appeared not to be affected by salinity, grain size, and pore water which have been shown to affect distribution on north European and South African beaches (Jansson 1968, Mielke 1976, McLachlan 1980).

Various parts of the world have a zonal distribution of macrobenthos on rocky shores in common. Generally there are three zones: a littorinid/black lichen zone (upper); a barnacles zone (middle); and a zone of large brown algae or ascidians and red algae (lower). In spite of many studies (see review in Raffaelli *et al.* 1991), a universal horizontal distribution on sandy shores has not been found. The present study reports an investigation of the distribution of meiobenthic copepods along three transects in Pauatahanui Inlet, New Zealand. Transects with different physical features were selected to investigate limiting factors to horizontal distributions and to determine whether any influence of physical features was uniform. In Pauatahanui Inlet the meiobenthic copepods, especially *Parastenhelia megarostrum*, have been extensively studied. The densities of *P. megarostrum* are affected by microtopographic (sediment ripples) and macrofaunal disturbance agents and tidal exposure (Hicks 1984, 1992).

Materials and Methods

Study site

Pauatahanui Inlet is located 20 km north of Wellington, New Zealand (Fig. 1). Intertidal flats and banks occupy about one quarter of the total area (about 1 km^2) of the Inlet (Healy 1980). The eastern inland end of the Inlet is a salt marsh where the sea rush, *Juncus maritimus*, forms dense mats that give way to a muddy sand beach whose surface supports large numbers of the pulmonate mud snail, *Amphibola crenata*. The western end is dominated by the silty sand of Mana Bank with extensive patches of eelgrass, *Zostera capricornii*, the green alga *Enteromorpha* spp., and a high density of venerid cockles, *Austrovenus stutchburyi*. The south bank slopes steeply into the main drainage channel of the Inlet.

A series of six to ten stations was sampled along each of the three transects extending from the intertidal zone into subtidal drainage channels. The stations were not regularly spaced along each transect, but instead were located to permit sampling of different sediment features, i.e., vegetation, tidal exposure, and water depth. The characteristics of each station are shown in Table 1.

Sampling scheme

Samples were collected during daylight hours at low tide at Transects 1 (T1) and 2 (T2) on 16 August and at Transect 3 (T3) on 17 August 1989. Both sampling days coincided with spring tides. Duplicate samples were collected at each sampling station, comprising 0.25 m^2 quadrats on either sides of the transect line. Quantitative samples were taken from each quadrat by hand coring with a plastic tube of 23 mm internal diameter (4.15 cm^2) to the depth of the redox layer (usually <5-6 cm). Each sample was washed into a plastic bag with a 10% formalin-Rose Bengal solution, and in the laboratory decanted through a 63 µm sieve.

An additional sample for grain size analysis

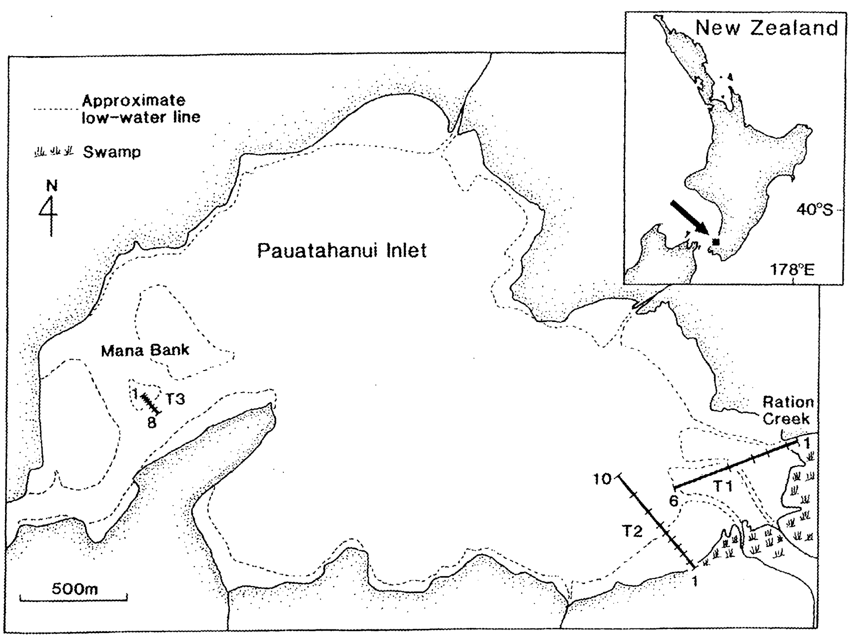

Figure 1 Sampling locations in the Pauatahanui Inlet, New Zealand. Small bars which intersect the transect lines (T1-T3) at right angles indicate sampling stations (1-6, 1-10 and 1-8, respectively).

was taken from one of either quadrats at each station and analysed after Barrett & Brooker (1989).

Data analysis

To evaluate the copepod community, species diversity H' (Shannon & Weaver 1949) was calculated. The density, number of species and H' are presented as the average of two quadrats (cores), because there is little difference between duplicate samples at each station. The ratios of duplicate samples were 1.06 to 5.60 (average 2.37) in the number of copepods and 1.0 to 3.0 (average 1.70) in the number of species. The data were also subjected to cluster analysis by the group average method using Simpson's coeffi-

Table 1 Summary of sampling location at Pauatahanui Inlet, New Zealand.

Station	Water depth at the low tide	Substrate	Granular variation (%)[1]				Median
			Gravel	Sand	Silt	Clay	diameter (mm)
Transect 1 (T1)							
T1-1	Exposure	Intertidal *Juncus* mudflat	0	24.6	40.2	35.3	0.01
T1-2	Exposure	Intertidal shore pimpernel, *Samolus*, mudflat	0.1	62.9	20.4	16.9	0.08
T1-3	Exposure	Intertidal sandflat	0	85.1	10.1	4.8	0.10
T1-4	Exposure	Intertidal sandflat	0	93.1	3.7	3.2	0.13
T1-5	Water's edge	Intertidal sandflat	0	95.6	2.1	2.3	0.14
T1-6	30 cm	Subtidal sand bottom	2.2	92.6	2.7	2.5	0.15
Transect 2 (T2)[2]							
T2-1	Exposure	Intertidal sandflat	0.6	96.1	2.8	0.5	0.33
T2-2	Exposure	Intertidal sandflat	1.2	81.9	9.9	7.1	0.12
T2-3	Exposure	Intertidal sandflat	0.7	88.5	5.8	5.0	0.11
T2-4	Exposure	Intertidal sandflat	0	96.3	1.8	1.9	0.14
T2-5	Exposure	Intertidal sandflat	0.1	97.5	0.9	1.6	0.16
T2-6	Exposure	Intertidal sandflat	0	98.0	0.7	1.3	0.16
T2-7	Exposure	Intertidal sandflat	0	98.4	0.6	1.0	0.19
T2-8	20 cm	Subtidal sand bottom	0	97.8	0.8	1.4	0.18
T2-9	1 m	Subtidal sand bottom	0	79.5	12.0	8.5	0.09
T2-10	2 m	Subtidal sand bottom	0	26.3	44.5	29.2	0.02
Transect 3 (T3)							
T2-1	Exposure	Intertidal sand beneath dense *Zostera* bed	0	86.3	7.4	6.4	0.12
T3-2	Exposure	Intertidal sand beneath dense *Entermorpha* bed	0	89.4	6.1	4.4	0.12
T3-3	Exposure	Intertidal bore sand	0	92.0	4.5	3.5	0.11
T3-4	Exposure	Intertidal sand beneath sparse *Zostera* bed	0	93.5	3.5	3.1	0.12
T3-5	50 cm	Subtidal sand bottom	0.2	93.2	3.7	2.9	0.13
T3-6	1 m	Subtidal sand bottom	0	91.5	4.2	4.3	0.13
T3-7	2 m	Subtidal sand bottom	0.1	94.1	3.2	2.6	0.13
T3-8	3 m	Subtidal sand bottom	0.1	94.5	2.7	2.7	0.13

[1]Grain size: Gravel, >2 mm; Sand, 2 - 1/16 mm; Silt, 1/16 - 1/256 mm; Clay, <1/256 mm

[2]St T2-1 to St T2-7 were positioned at 50 m intervals

cient (Simpson 1943) as the measure of similarity.

Results

Distribution and community structure

A total of 1489 specimens were collected. Of these, 1458 were identified as belonging to 29 species, the remainder being unidentifiable copepodites (Table 2). All species except *Halicyclops* sp. (Cyclopoida) belong to the Order Harpacticoida.

On transects in T2 and T3 the number of individuals, number of species and H' tended to increase significantly with depth (Fig. 2). Spearman's rank correlation coefficients of the number of individuals, number of species and H' with depth were respectively: 0.770 ($P<0.01$), 0.880 ($P<0.01$) and 0.585 ($P<0.05$) for T2, and 0.905 ($P<0.01$), 0.976 ($P<0.01$) and 0.887 ($P<0.01$) for T3. In T1 no significant correlation was found.

Sampling stations were compared in two types

Table 2 Species list of meiobenthic copepods collected from Pauatahanui Inlet, New Zealand.

Order	Family	Species
Cyclopoida	Cyclopidae	*Halicyclops* sp.
Harpacticoida	Canuellidae	*Brianola* sp.
	Ectinosomatidae	*Halectinosoma hydrofuge*
		Halectinosoma otakoua
		Bradya sp.
		Psudobradya sp.
		Noodtiella sp.
		Ectinosomatidae sp.
	Harpacticidae	*Harpacticus* sp.
	Porcellidiidae	*Porcellidium* sp.
	Thalestridae	*Paradactylopodia brevicornis*
	Parastenheliidae	*Parastenhelia megarostrum*
	Diosaccidae	*Stenhelia* (*Stenhelia*) sp.
		Stenhelia (*Delavalia*) *oblonga*
		Robertsonia propinqua
		Bulbamphiascus sp.
		?*Paramphiascella* sp.
		Schizopera sp.
		Cladorostrata sp.
		Miscegenus heretaunga
	Ameiridae	*Nitocra* sp.
	Leptastacidae	*Sextonis* sp.
	Cletodidae	*Enhydrosoma variabile*
		Cletodidae sp.
	Laophontidae	*Laophonte inornata*
		Laophonte sp.
		Paralaophonte aenigmaticum
		Quinquelaophonte candelabrum
		Laophontidae sp.

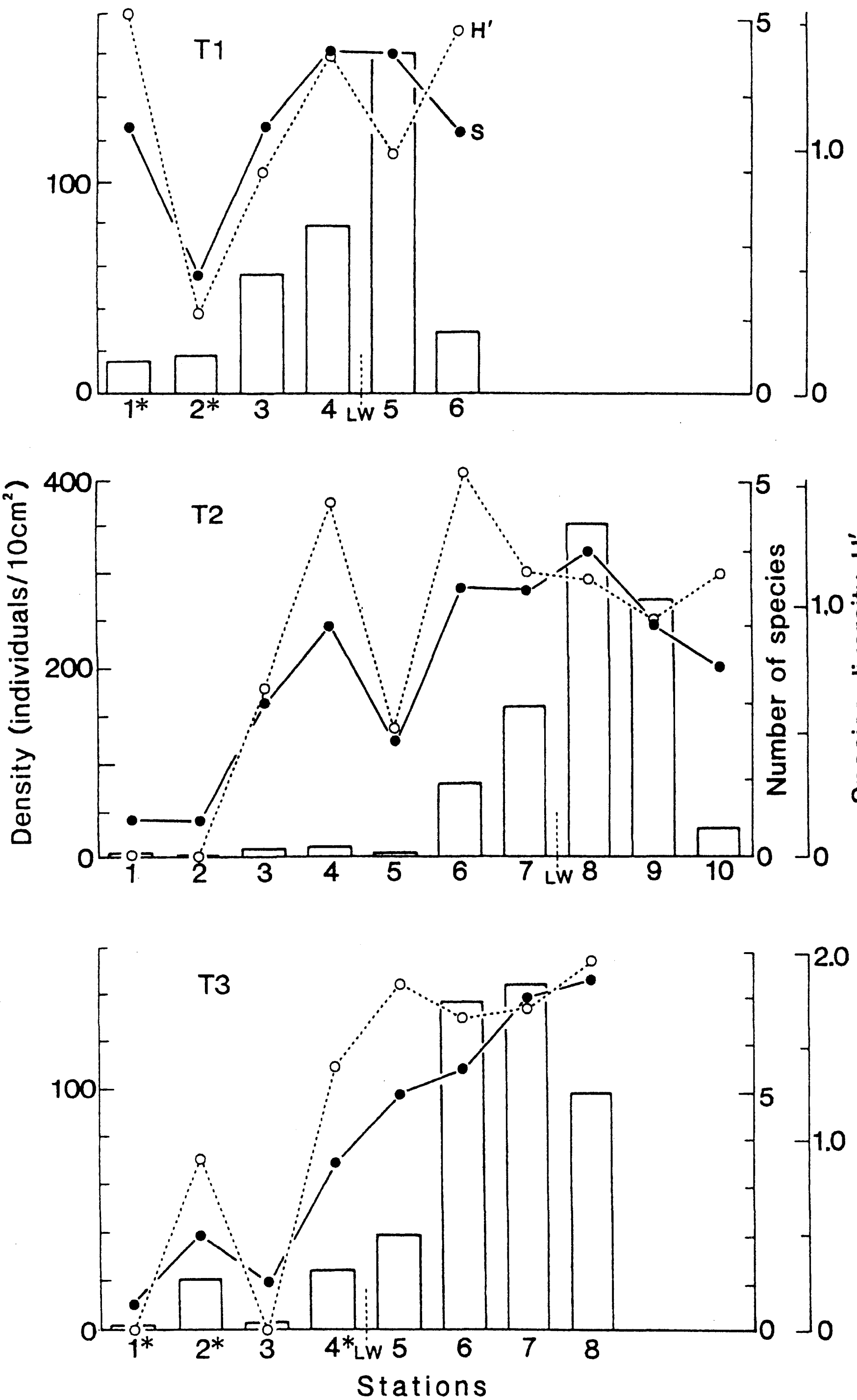

Figure 2 Mean numbers per 10cm^2 (histograms), number of species, S (filled circles) and diversity, H' (open circles) of meiobenthic copepods in Pauatahanui Inlet. Asterisks, vegetated sediments: LW, low-water level.

of habitat segregation: intertidal versus subtidal zones, and intertidal vegetated versus bare sediments. The number of individuals, number of species, and H' were significantly higher in the subtidal than in the intertidal zone. There were no significant differences in all indices between vegetated and bare sediments in the intertidal zone (Table 3).

Each transect differs in the zonation patterns of its abundant copepods. On T1 (Fig. 3A) *Halectinosoma hydrofuge* dominated, comprising 63.6-83.0 % of the total numbers on the sandflat and at the water's edge (Stn T1-3 to T1-5). *Robertsonia propinqua* was the next most abundant species at these stations. *Stenhelia* (*Stenhelia*) sp. was abundant on intertidal sediments, especially at T1-2. In T2 there was a major change in dominant species between Stn T2-8 and Stn T2-9, with *P. megarostrum* and *Sextonis* sp. comprising over 92% of the total at Stns T2-6 to T2-8 and *Brianola* sp. and *H. hydrofuge* comprising 98.6% at Stn T2-9 (Fig. 3B). At T3 *Halectinosoma otakoua*, *Parastenhelia megarostrum* and *Stenhelia* (*St.*) sp. were dominant in the subtidal area (Fig. 3C).

The profiles in T2 and T3 indicated distinct zonation patterns of the meiobenthic copepods. The water depth influenced the zonation patterns. However, there was no particular substrata copepods, which were distributed more than one transect, preferred except *Paralaophonte aenigmaticum*. *P. aenigmaticum* occurred in subtidal zones in T1 and T2. Concerning the vegetation, four species, *Nitocra* sp., *Schizopera* sp., *Cladorostrata* sp. and Cletodidae sp., were restricted to *Juncus* mud in T1 (Stn T1-1). However, *Schizopera* sp. was distributed in sandflats in T2 (Stn T2-3 and T2-4). In T3 there was no species distributed in only vegetated sediments.

Cluster analysis demonstrated that similarities between stations were very low: only two clusters, each of two or three neighbouring stations, appeared at the 0.8 level of Simpson's coefficient. One cluster, at 0.86, comprises Stn T1-4 and T1-5, where *H. hydrofuge* and *R. propinqua* were dominant. The second, at 0.80, comprised Stn T2-6, T2-7, and T2-8, where *P. megarostrum* and *Sextonis* sp. comprised more than 90% of the copepod fauna.

Grain size and distribution of copepods

The sediment at most intertidal stations (and subtidal stations at T3) was sand with a small proportion of silt and clay, St T1-1 and T1-2 excepted (Table 1). By contrast, subtidal sediments at the eastern end of the Inlet (St T2-8 to St T2-10) contained far more silt and clay. A relationship exists between granulometric composition of the sediment and the abundance of the four species at T2, with *Sextonis* sp. and *P. megarostrum* occurring in fine, clean sand and

Table 3 Comparisons of copepod density, number of species, and diversity (H') between intertidal and subtidal zones, and vegetated and bare sediments in the intertidal zone of Pauatahanui Inlet, New Zealand. There are significant differences in the density, number of species and H' between intertidal and subtidal zones (one-way ANOVA $P<0.01$).

	Density (inds/10cm^2)		Number of species		H'		Number of samples
	Mean	SD	Mean	SD	Mean	SD	
Intertidal vs. subtidal zones							
Intertidal zone	32.7	44.0	2.3	1.3	0.77	0.60	15
Subtidal zone	140.7	110.7	4.7	1.7	1.42	0.38	9
Vegetated vs. bare sediments							
Vegetated sediments	16.2	9.3	2.2	1.3	0.81	0.65	5
Bare sediments	41.0	52.3	2.4	1.4	0.75	0.61	10

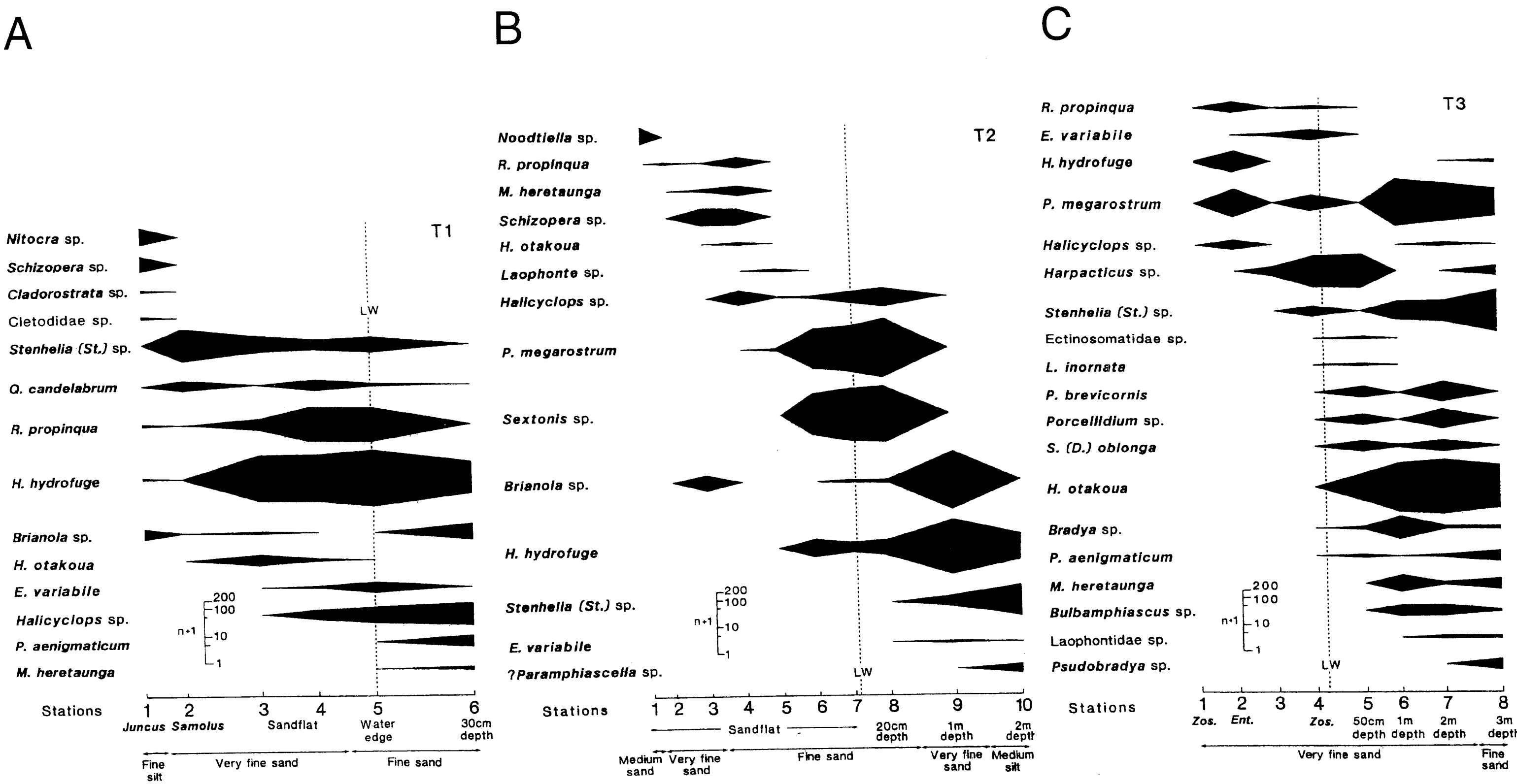

Figure 3 Distribution of meiobenthic copepods on Transect 1- 3 (Fig. 3A-C) in the Pauatahanui Inlet. Mean copepod numbers per 10cm^2; LW, low-water level, depths indicate water depths at low tide.

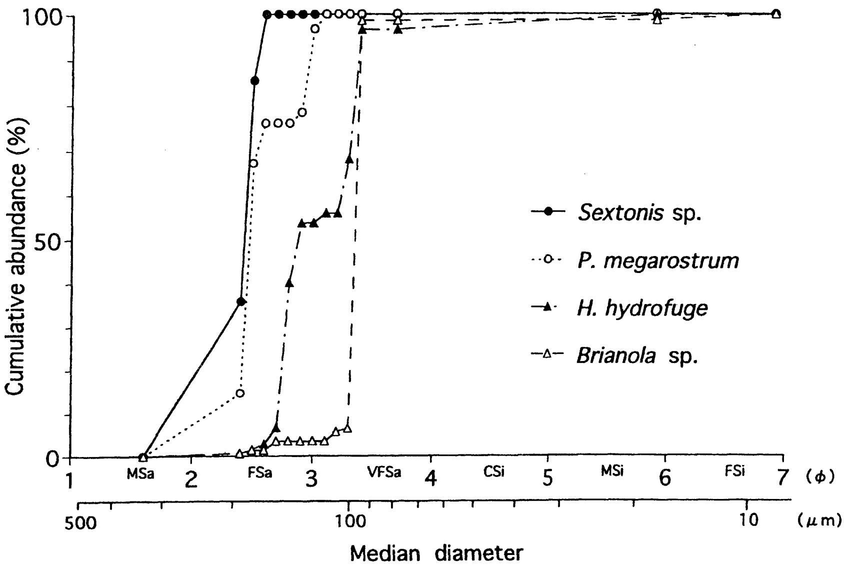

Figure 4 Cumulative curves of the numbers of the four abundant meiobenthic copepod species versus the median diameter of sediments. MSa, medium sand; FSa, fine sand; VFSa, very fine sand; CSi, coarse silt; MSi, medium silt; FSi, fine silt.

H. hydrofuge and *Brianola* sp. in substrata with a higher silty/clay content (Fig. 4). In contrast, a similar relationship was not observed on transects T1 and T3.

Discussion

Cluster analysis of the species composition in the present study did not reveal any consistent groupings. Nevertheless there were clear patterns of horizontal distribution along each transect - possibly owing to a gradient of environmental stability from the intertidal to subtidal zones.

Sediment grain size appeared to regulate the distribution of some harpacticoid copepods on T2, confirming conclusions in previous studies (Soyer 1970, Gray 1974, Moore 1979c, Ivester 1980). Moore (1979a) showed that the density of interstitial harpacticoid copepods declines in sediment below 2.61ϕ (0.164 mm) mean diameter . Hockin (1982) reported that densities of *Evansula incerta* and *Arenosetella germanica* were higher in fine sediments (0.147 and 0.267 mm particle diameters), whereas densities of *Arenopontia subterranea* and *Arenosetella tenuissima* were higher in coarser sediments (0.367 and 0.485 mm particle diameter) in field experiments using four kinds of artificial monometric sediments.

The present study indicated that harpacticoid copepods can be associated with certain grain sizes (Fig. 4). In T2, *P. megarostrum*, and *Sextonis* sp. were associated with fine sand (0.17-0.19 mm median diameter) whereas *H. hydrofuge* and *Brianola* sp. were associated with silt and finer sand (0.02-0.10 mm median diameter). The correlation between the grain size and the distribution of copepods was distinct on T2 because the substrata and grain size gradients were more homogeneously distributed and steeper than in T1 and T3.

Brown & McLachlan (1990) presented a response model of sandy beach meiofauna to a particle size gradient, with 0.18-0.20 mm median diameter being critical for harpacticoid fauna: burrowing copepods were abundant in sand finer than 0.18-0.20 mm, and interstitial copepods in sand coarser than 0.18-0.20 mm. The present study is in agreement with their model except that *P. megarostrum* is not interstitial. The response of harpacticoid copepods to the particle size gradient is particularly clear at T2 where a wide range of particle sizes occurred (Table 1).

Spatial heterogeneity (Bell 1979, Coull *et al.* 1979) and environmental stability (Hartzband & Hummon 1974) are thought to be major determining factors of community structure, which can be expressed in terms of density and species diversity. The spatial heterogeneity which is caused by macrovegetation increases habitable space, colonization sites and refuges for the meiofauna (Bell *et al.* 1978). The present study showed that copepod density tended to increase significantly with depth on two transects. The depth may indicate environmental stability, that is the intertidal zone is more unstable than the subtidal zone due to the tidal exposure. It was expected that copepod density would also be high in vegetated sediments because of enhanced spatial heterogeneity, but this was not observed (Fig. 2, Table 3). High density appeared to be maintained by the stability of the environment, rather than by spatial heterogeneity.

Species diversity has been shown to be dependent on environmental factors: substrate, grain size, and presence or absence of vegetation (Coull & Fleeger 1977, Bell 1979, Fleeger 1980, Hockin 1982, Hicks & Coull 1983). In the present study, the number of species and H' increased significantly with depth on two transects, but there was no difference between vegetated and bare sediments (Fig. 2, Table 3). Again, environmental stability appears to have a greater influence on H' than has spatial heterogeneity.

Although previous studies have shown that the number of species is lower in the sand ripples of Mana Bank than in a featureless surface (Hicks 1986), no significant difference in diversity was found between the subtidal bottom of Mana Bank, where there are sand ripples, and the featureless surface of sand bottom in Ration Creek (Iwasaki 1993).

Previous studies (Hicks 1986, Bell & Hicks 1991) showed *Harpacticus* sp., *Laophonte inornata*, *Paradactylopodia brevicornis* and *Porcellidium* sp. to be the typical phytal species, and *Bulbamphiascus* sp. the most abundant species on subcanopy sediments in Mana Bank. In the present study, however, these species were found on bare subtidal sediments, except for *Harpacticus* sp., which appeared in intertidal and subtidal sediments (Fig. 3C). Phytal species are known to migrate into the water column (Bell *et al.* 1988) so these species can be expected to be collected from subtidal sediments in low numbers. The occurrence of phytal species in bare subtidal sediments may have resulted from resettlement away from their preferred substratum (Bell *et al.* 1989).

Hicks (1984) showed that *P. megarostrum* attains intertidal densities of 618.2 ± 400.1 per 10 cm^2, among the highest of any meiobenthic copepod world-wide. In the present study, such high densities were not observed and *P. megarostrum* was even more abundant in subtidal sediments than in intertidal sediments (Fig. 3B, C). The mean density in intertidal sediments in the present late winter study (7.2 ± 17.0 per 10 cm^2) is lower than the lowest density during Hicks' 14 month study (42.4 ± 10.8 per 10 cm^2), most likely because the present study did not sample ripple troughs where densities of *P. megarostrum* are very much higher than on crests and in adjacent featureless sand (Hicks 1984, 1986). And Hicks (1984) showed the densities of *P. megarostrum* were low in late summer and autumn (February-April) and high in June-July, September, November and January. The densities in late winter were almost the same level as the mean density of the fourteenth month.

In conclusion, the presence of vegetation, tidal exposure, or water depth were not common factors governing species distribution in Pauatahanui Inlet in late winter. The zonal distribution and community structure were influenced by water depth exposure in two out of three transects. And grain size was correlated with species distribution on the transect in which the grain size gradients were distinct.

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